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A SYSTEMATIC TREATMENT OF THE *PHACELIA FRANKLINII* GROUP¹

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The New World genus *Phacelia* (Hydrophyllaceae) includes between 150 and 200 species (Constance, 1951) some native to South America; but the majority being restricted to North America, occurring from Guatemala to within 50 miles of the Arctic Circle. Brand (1913) divided the genus into six sections, four of these sections being relatively small and together comprising 33 species. The remaining two sections are comparatively large and nearly equal in size. One of these larger groups, the section *Eutoca*, is exclusively North American and is distinguished by corolla scales and the presence of more than four pitted seeds per capsule. The section *Eutoca* is probably an artificial assemblage of relatively distinct species groups. One of these, herein referred to as the *Phacelia Franklinii* group, is an aggregation of six montane to alpine to sub-arctic species. In addition to *P. Franklinii*, the group includes *P. Lyallii*, *P. lenta*, *P. mollis*, *P. idahoensis*, and *P. sericea*.

The current infra-generic classification of *Phacelia* is generally conceded to be inadequate. However, considerably more evidence must be accumulated before the various species groups can be accorded a classification that properly relates them to each other. It seems necessary, therefore, to defer the formal recognition of the *Phacelia Franklinii* group until enough knowledge is accumulated to make possible a realignment of the species groups of the entire genus.

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The growth pattern in these species is marked by the formation of a basal leaf rosette from which an inflorescence axis arises. Plants of *Phacelia Franklinii* are spring to summer-flowering biennials, or summer-flowering annuals; while those of *P. lenta*, *P. Lyallii*, *P. mollis*, *P. idahoensis*, and *P. sericea* are spring-flowering perennials. In distribution, the group extends from northern Arizona to Great Bear Lake, Canada, and from the Olympic Peninsula east to Lake Superior. Because of the variation and unreliability of the taxonomic characters previously employed in this group, an experimental study was initiated and evidence obtained from both living plants and herbarium specimens. All species, except *P. lenta* which is known only from the type collection, have been grown from seed.

The assistance of those who have obtained seed collections for this investigation is gratefully acknowledged. Appreciation is also extended to Dr. Lincoln Constance and to my colleagues Drs. Henry Imshaug and John Beaman for their discussions and criticisms. Special thanks are extended to the many herbarium curators who have made specimens available for this study. Herbaria are cited by the abbreviations of Lanjouw and Stafleu (1959).

TAXONOMIC HISTORY

The description of *Eutoca Franklinii* (and of the genus *Eutoca*) by Robert Brown (1823) marked the first recognition of a species in this group. Brown's description was based on material obtained in northern Saskatchewan by the first Franklin expedition. In 1830, Graham added the description of *Eutoca sericea*, based on material grown from seed collected in the Canadian Rockies by Drummond. These two species were illustrated in Curtis's Botanical Magazine in 1830, and have since been interpreted as distinct species.

Gray (1875) gave *Eutoca* subgeneric rank under *Phacelia*, and inferred a close relationship between *Phacelia Franklinii* and *P. sericea* by aligning them in a common group, at the same time describing *P. Lyallii* as a variety of *P. sericea*. Brand (1913) placed *P. Franklinii*, *P. lenta*, and *P. sericea* in the same group, and interpreted both *P. Lyallii* and *P. idahoensis* as subspecies of *P. sericea*.

Both *Phacelia linearis* and *P. procera* have been variously

aligned with species of the *P. Franklinii* group by Gray (op. cit.), Brand (op. cit.), and Howell (1945). To clarify these interpretations, both *P. linearis* and *P. procera* were included in certain aspects of this study.

MORPHOLOGY AND CYTOLOGY

MORPHOLOGICAL STUDIES. — *Flowers.* The corollas of most phacelias have linear appendages that are adnate along one edge to the inner surface of the corolla tube. Each appendage is fused to a lateral vein, there being two such appendages, or scales, at the base of each petal (Fig. 1). In *Phacelia linearis* and in species of the *P. Franklinii* group, these appendages are nearly parallel and are free of the stamen filaments. By contrast, the appendages of *P. procera* are strongly divergent and are fused across the filament bases, forming a pocket (Fig. 1-B). The appendages of *P. linearis* and of species of the *P. Franklinii* group overlie a nectary along the midvein, a feature that has been described by Constance (1949) in phacelias of the section *Cosmanthus*. The surface of this nectary is glabrous in *P. linearis* and in *P. Franklinii*, but is hairy in other species of the *P. Franklinii* group. The glabrous inner corolla surface and the numerous, long hairs of the stamen filaments generally distinguish the flowers of *P. Franklinii* from those of all other members of the *P. Franklinii* group. The glandular hairs on the lower portion of the stamen filaments of *P. linearis* suffice to distinguish this species from members of the *P. Franklinii* group.

Seeds. Seed-coat features have long been used in the classification of phacelias, and have proven useful in delimiting species of this study. These features are illustrated in Fig. 2. Seed-coat details were obtained from photographic enlargements on which the sculpturing detail was inked, with the remaining details subsequently bleached out. This technique revealed very subtle, but consistent differences in seed-coat sculpturing. The seed-coat sculpturing in *Phacelia linearis* is relatively coarse and is registered on the endosperm, while the sculpturing in other seeds is finer, and is restricted to the seed coat. The finely sculptured seed coat of *P. Lyallii* is most distinctive, and enables one to identify readily the seeds of this species when they are mixed with

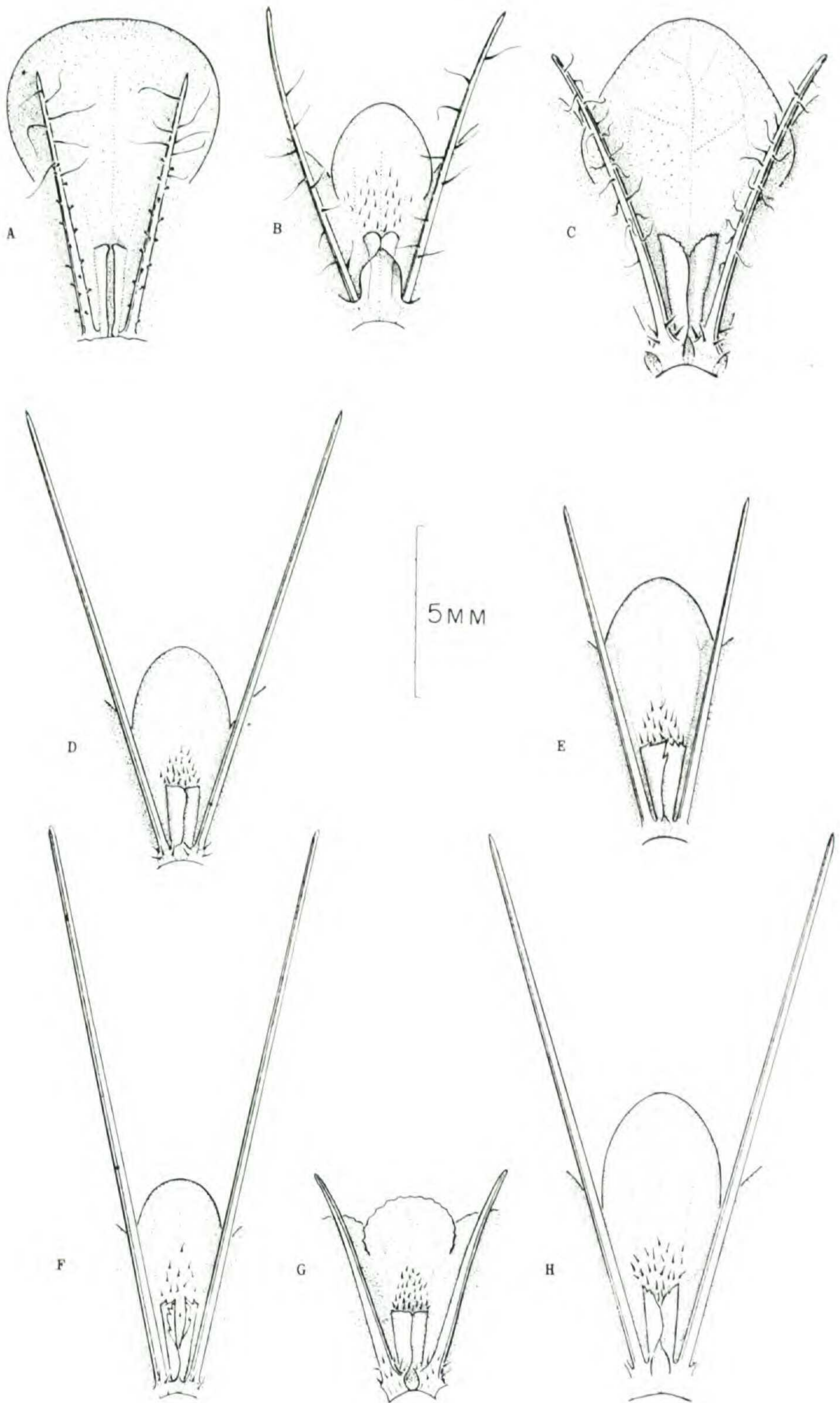


FIG. 1. Corolla morphology of: (A) *Phacelia linearis*, Preece 2262 (MSC); (B) *P. procera*, Richardson s.n. (ID); (C) *P. Franklinii*, Langenheim 4319 (MSC); (B) *P. sericea* subsp. *sericea*, Gillett 1149 (MSC); (E) *P. Lyallii*, TYPE; (F) *P. lenta*, TYPE; (G) *P. idahoensis*, Henderson 2770 (MSC); (H) *P. mollis*, Smith 2407 (MSC).

those of other species included in this study. The seed-coat detail of *P. Franklinii*, *P. sericea*, *P. mollis*, and *P. idahoensis* is so similar that I have been unable to distinguish consistently the seeds of a given species when they are mixed with those of the other three.

The internal morphology of seeds was described by Martin (1946), who presented evidence from over 1200 genera, including *Phacelia*, and *Hydrophyllum*. Martin found linear and spatulate embryos in *Phacelia strictiflora* and *P. californica*, respectively, and the dwarf type in *Hydrophyllum canadense*. His study would indicate that embryo morphology does little to distinguish the Hydrophyllaceae, for the embryo types he found occur in many other families.

In the present study, the internal morphology of seeds was studied by first boiling them in 3% NaOH, removing the loosened seed coats, and sectioning by hand. In addition to revealing differences in embryo size (Fig. 2), this technique brought out interesting differences in the reaction of the seed coats.

The embryo of *Phacelia Lyallii* is comparable to the dwarf type described by Martin, and is the most distinctive type found in this group. Embryos of the other species are of the spatulate type; that of *P. linearis* being distinctive in its large size (Fig. 2-B). While the seeds of *P. procera* are consistently larger than those of the other species, the embryos are similar in size and shape. In general, embryo features do not distinguish these species as well as do seed coat details.

The boiling of seeds in 3% NaOH brought out differences in the chemical properties of the seed coats. The seeds of *Phacelia mollis* left a colorless solution, while those of all other species imparted a brown color to the NaOH solution. Seeds of *P. Lyallii* were distinctive in their sloughing, intact, the outer seed coat after this treatment. By contrast, the outer seed coat of other species came off in fragments that were often difficult to remove. The outer seed coat of *P. Franklinii* came off in large fragments, leaving a persistent, opaque inner seed coat. After the removal of the inner seed coat, the endosperm appeared translucent, and the embryo was revealed in detail. By contrast, the endosperm of all

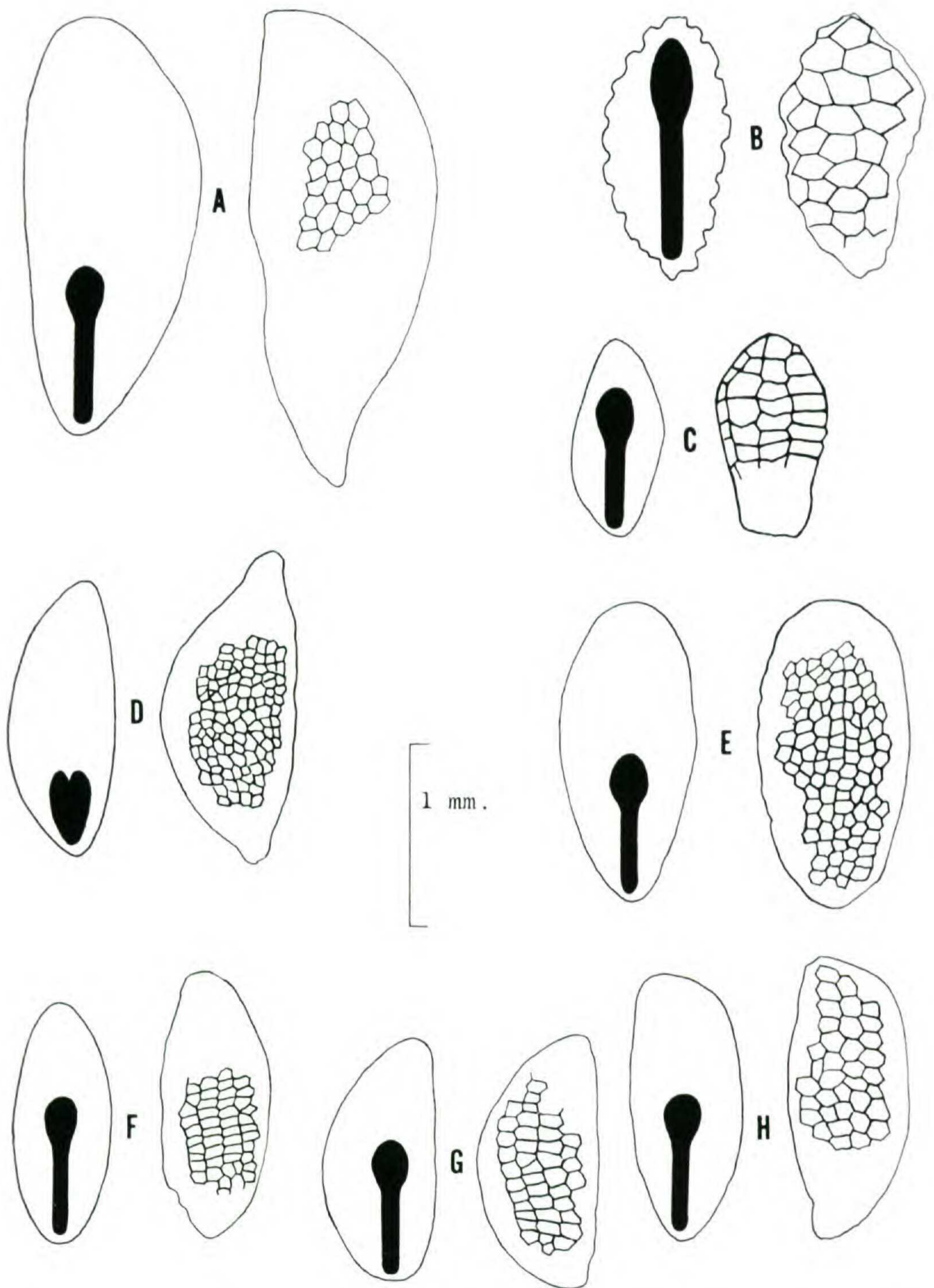


FIG. 2. Seed-coat sculpturing (right), and embryo morphology (left) in: (A) *Phacelia procera*, Pollard s.n. (CAS); (B) *P. linearis*, Hedgecock s.n. (GH); (C) *P. lenta*, TYPE; (D) *P. Lyallii*, Bailey s.n. (CAS); (E) *P. Franklinii*, Langenheim 4319 (MSC); (F) *P. mollis*, Scamman 6324 (GH); (G) *P. sericea* subsp. *sericea*, Meyer 1080 (GH); and (H) *P. idahoensis*, Gillett 1147 (MSC).

other species was opaque. A meaningful interpretation of these differences awaits a definitive histochemical study that is not within the scope of this investigation.

Trichomes. — Glandular trichomes are very common in phacelias, and were discussed by Brand in his monograph of the Hydrophyllaceae (op. cit.), and by Gillett (1955). In this study, glandular hairs (colleters) have been observed on the herbage, calyces, and (in *P. linearis*) stamen filaments. The glandular hairs that characterize a given species were drawn from the sepal margins (Fig. 3).

The multicellular head of the glandular hairs of *Phacelia procera* aids in distinguishing this species from *P. linearis*, and from all members of the *P. Franklinii* group. All other species are characterized by glandular hairs having unicellular heads. In *P. lenta*, the elongate stalk cells of the glandular hairs are a distinguishing feature.

The tapering trichomes of the *Phacelia Franklinii* group exhibit a wide range in size, an attribute Heckard (1960) has cited for the tapering trichomes in species of the *P. magellanica* complex. However, one species, *P. Lyallii*, has an indument that includes relatively large tapering trichomes, these giving a distinctive harsh texture to the herbage, in contrast to the soft-textured herbage of *P. sericea*.

The measurement of the large tapering trichomes on the calyces of *P. Lyallii* and *P. sericea* reveals a difference in trichome diameter that probably accounts for the contrast in surface texture in these species. These data are given in table 1.

The initial comparison of the stomates of *Phacelia Lyallii* and *P. sericea* indicated that there might be a gross difference in the length of the guard cells in these two species. Accordingly, 50 stomates were measured on the calyces of each species and are reported in table 1. The comparison of guard cell lengths does not reveal the significant difference that was suspected. It is nevertheless interesting to see that a great difference in trichome size and a lesser difference in guard-cell length occurs in two closely related *diploid* species.

CYTOLOGY. — The determination of chromosome numbers in both subspecies of *Phacelia sericea* was accomplished by

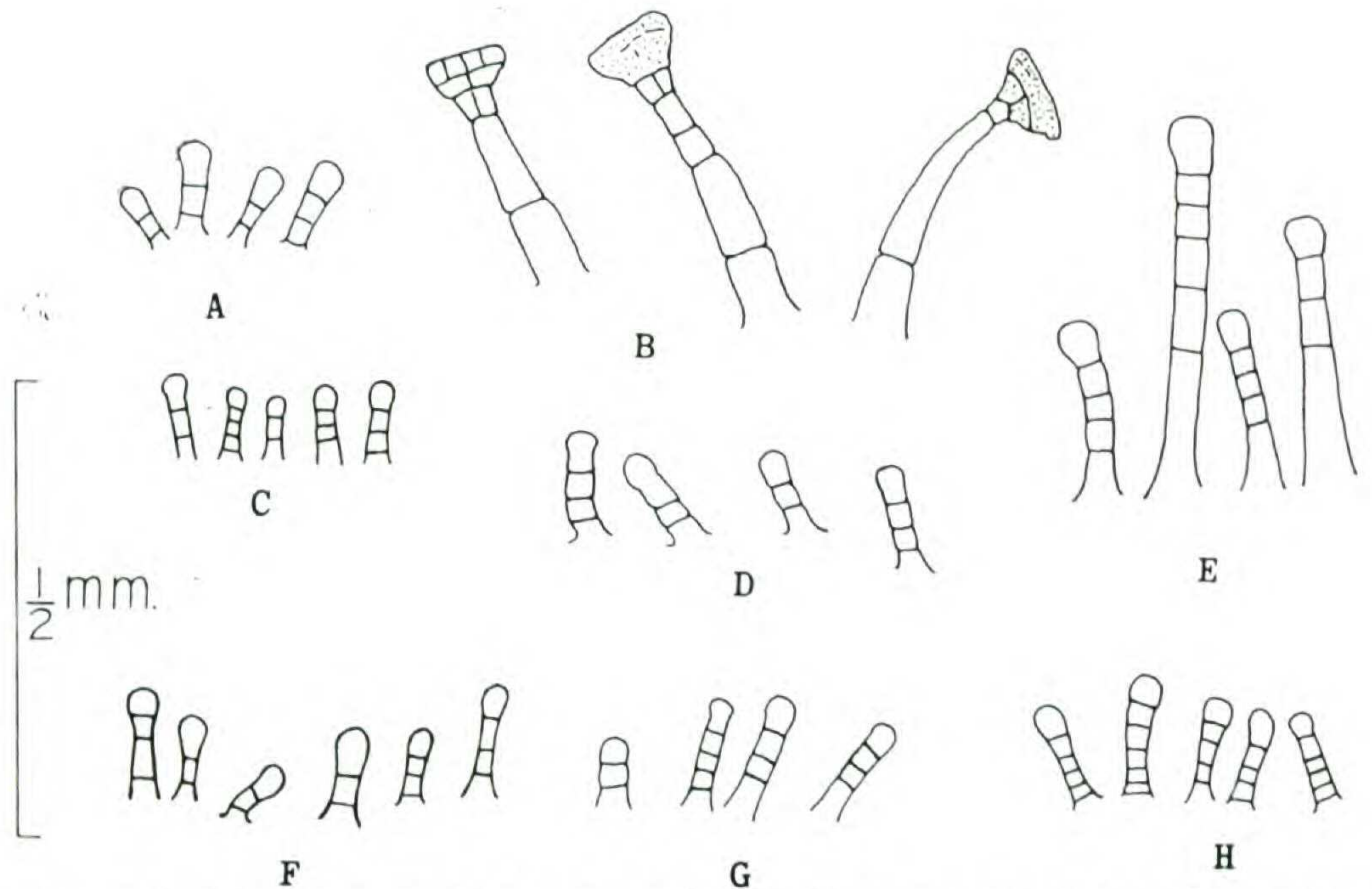


FIG. 3. Colleter types of: (A) *Phacelia Lyallii*, Gillett 1151 (UC); (B) *P. procera*, Richardson s.n. (ID); (C) *P. sericea* subsp. *sericea*, Gillett 1149 (MSC); (D) *P. linearis*, Preece 2262 (MSC); (E) *P. lenta*, TYPE; (F) *P. idahoensis*, Cronquist 2337 (GH); (G) *P. Franklinii*, Raup 3020 (GH); and (H) *P. mollis*, Smith 2407 (MSC). Cave and Constance (1942, 44, 47, 50, and 59). Their counts were made of the following material:

	Chromosome No.	Document
<i>Phacelia sericea</i> subsp. <i>sericea</i>		
Montana, Glacier Co.	n = 11	Cave 4115 (UC).
Wyoming, Albany Co.	n = 11	Beetle 4703 (UC).
Colorado, Larimer Co.	n = 11	Beetle 4726 (UC).
<i>Phacelia sericea</i> subsp. <i>ciliosa</i>		
Wyoming, Uinta Co.	n = 11	Constance 3209 (UC).
Nevada, Elko Co.	n = 11	Maguire & Holmgren 22303 (UC).

Chromosome counts for other species of this group were determined in the present study. These include:

<i>Phacelia Lyallii</i>		
Montana Glacier Co.	n = 11	Gillett 1151 (UC).
<i>Phacelia Franklinii</i>		
Yukon (Teslin Lake)	n = 11	Gillett 1185 (UC) (from Langenheim 4319).
<i>Phacelia idahoensis</i>		
Idaho, Valley Co.	n = 11	Gillett 1147-1 (UC) (from Hockaday s.n. (UC).
<i>Phacelia mollis</i>		
Alaska (Haines)	2n = 22	Rude s.n. (MSC)

The uniform occurrence of eleven pairs of chromosomes by no means distinguishes the *Phacelia Franklinii* group

from other phacelias. Cave and Constance (op. cit.) have found this chromosome number in no less than 75 species, these representing five of Brand's six sections.

TABLE 1. Size comparisons of guard cells and large trichomes on sepals of *Phacelia sericea* subsp. *sericea*¹ and *P. Lyallii*².

	No. Measured	MICRONS		
		Min.	Median	Max.
Guard Cell Length				
<i>P. sericea</i> subsp. <i>sericea</i>	50	23	28	39
<i>P. Lyallii</i>	50	26	36	42
Trichome Diameter (Basal)				
<i>P. sericea</i> subsp. <i>sericea</i>	50	27	35	50
<i>P. Lyallii</i>	50	50	62	95

¹Gillett 1162-1 (MSC).

²Gillett 1151 (UC).

TAXONOMIC TREATMENT

The *Phacelia Franklinii* group: — Erect annuals, biennials, or perennials forming leaf rosettes upon germination; an inflorescence axis arising from the center of the leaf rosette, bearing a congested, terminal, virgate or spreading inflorescence; corolla tube with overlapping, near-parallel corolla scales covering a nectary at the base of each petal, each scale adnate along one edge to a lateral vein, the free edge overlying the midvein; capsule with 10-60 reticulately pitted seeds.

Species 6, northern Arizona to Great Bear Lake, Canada.

KEY TO THE SPECIES

- Annuals or biennials with hairy filaments; inner surface of corolla glabrous; up to 40-60 seeds per capsule 1. *P. Franklinii*.
- Perennials with glabrous filaments; inner surface of the corolla pubescent; 10-40 seeds per capsule.
- Plants glandular; restricted to south-central Washington 2. *P. lenta*.
- Plants not glandular.
- Hairs coarse, giving a rough strigose texture to herbage; inflorescence non-virgate; restricted alpine 3. *P. Lyallii*.
- Hairs fine, giving a soft texture to herbage; inflorescence virgate. Pubescence of spreading hairs, giving a velutinous herbage; Alaska & Yukon 4. *P. mollis*.
- Pubescence of appressed hairs; herbage glabrate to sericeous; northern Arizona to central British Columbia.
- Leaves coarsely lobed, glabrate; corollas urceolate; stamens ca. 1¼ length of corolla; central Idaho 5. *P. idahoensis*.
- Leaves with broad to narrow lobes, light to densely sericeous; corollas urceolate-campanulate to campanulate; stamens 1¼ -

- 3 times length of corolla; Arizona to British Columbia
 6. *P. sericea*.
 Stamens 2 - 3 times length of corolla; corollas campanulate;
 leaves with narrow lobes, sericeous to densely sericeous
 6-A. subsp. *sericea*.
 Stamens 1¼ - 2 times length of corolla; corollas urceolate-
 campanulate; leaves with broad lobes; light-sericeous
 6-B. subsp. *ciliosa*.

1. **Phacelia Franklinii** (R. Br.) A. Gray, Man. Bot. ed. 2, 329. 1856.

Eutoca Franklinii R. Brown in Richards. Bot. App. Franklin Journey 764, t. 27. 1823. Bot. Mag. 57:pl. 2985. 1830.

Annual or biennial 1-10 dm tall, with pubescence of straight, simple hairs and interspersed glandular hairs; initial vegetative axis 1-3 cm long; one or more leafy aerial branches arising from the rosette and terminated by inflorescences; leaves 5-15 cm long, the petioles 1-4 cm; blades lanceolate to ovate, pinnatifid to pinnate, the linear to ovate divisions entire to coarsely toothed to deeply lobed; branches terminated by smaller laterals, each bearing one or two cymes up to 15 cm. long; flowers on stout, glandular pedicels 1-2 mm long; the linear calyces 5-10 mm long, equal to the mature capsule; corolla deciduous, 10-15 mm long, campanulate, divided nearly one-half its length into tapering, rounded, violet, lavender, or white lobes, inner surface glabrous; tube white, stamens equal to corolla, the filaments with numerous to few tapering, contorted hairs on upper portion, with few short, erect hairs at bases; style equal to filaments, cleft about one-third its length, with glandular and non-glandular hairs on lower portion; capsule 5-10 mm long, acute; seeds 40-60, black, ca. 1.5 mm long.

TYPE AREA: Churchill River, northern Saskatchewan (Richardson, 1st Franklin Exped.).

RANGE: Wyoming, northwest to the central Yukon and Great Bear Lake, east to Hudson Bay and the north shore of Lake Superior, sea level to 8,000 feet (Fig. 4).

Phacelia Franklinii is perhaps the most widely distributed species in the genus. It remains relatively uniform throughout its range, with slight variations in flower color and in frequency of filament hairs.

A close relationship between *Phacelia Franklinii* and *P. linearis* has been postulated by Gray (1875), and Howell (1945). However, a point-by-point comparison of these two species in terms of corolla morphology, pubescence of filaments, seed-coat sculpturing, and embryo structure (Figs. 1 & 2) reveals conspicuous qualitative differences that suggest a distant, rather than a close relationship. Furthermore, *P. linearis* is a strict annual, while *P. Franklinii* demonstrates the biennial as well as the annual duration. Finally, numer-

ous reciprocal cross-pollinations between greenhouse plants of *P. Franklinii* (Gillett 1185 (UC)) and *P. linearis* (Preece 2262 (MSC)) all failed to produce seed.

MACKENZIE DISTRICT: Great Bear Lake, *Porsild* 3707 (CAN). YUKON: Lewes River, 62°, *Ogilvie* 17012 (CAN); Mile-Post 841, Alaska Highway, *Langenheim* 4319 (UC, MSC). ALASKA: Skagway, *Eyerdam* 3334 (UC). BRITISH COLUMBIA: Iskut River, *Preble & Mixter* 604 (US); Redstone, *Eastham* 12285 (UBC, UC, WS, CAN). ALBERTA: Athabasca Lake, *Raup & Abbe* 4479 (CAN, GH); Pyramid Lake, Jasper Park, *Scamman*

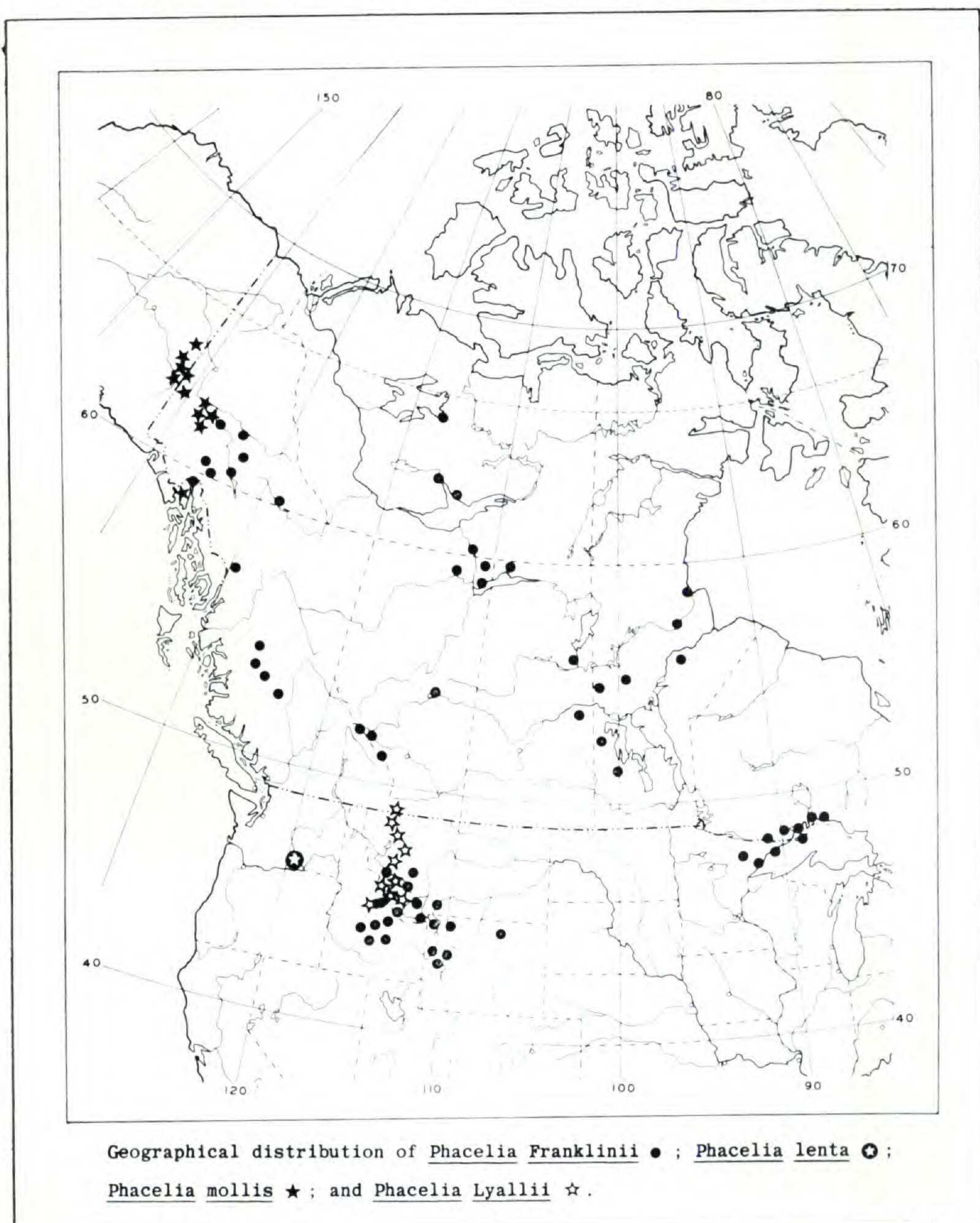


FIG. 4. Geographical distribution of *Phacelia Franklinii*, *P. lenta*, *P. mollis*, and *P. Lyallii*.

3019 (GH, US). SASKATCHEWAN: Hudson Bay Junction, *Breitung 1003* (CAN, UC). MANITOBA: Churchill, *Gardner 89* (CAN); Riding Mountains, *Halliday s.n.* (CAN). ONTARIO: Nipigon River, *Macoun s.n.* (CAN). MINNESOTA: Cook Co.: Mountain Lake, *Butters et al. 118* (GH, US, MIN). MICHIGAN: Isle Royal, Rock Harbor Light, *Cooper 96* (MIN). IDAHO: Custer Co.: Mackay, *Nelson & Macbride 1468* (CAN, GH, MIN, RM, US, WS, UC). MONTANA: Beaverhead Co.: Wisdom, *Hitchcock & Muhlick 12594* (UC, GH, US, RM, WS, CAN, PH). WYOMING: Sublette Co.: Green River Lakes, *Porter 5551* (CAS, UC, PH, US, RM, GH); Washakie Co.: Ten Sleep Canyon, *Nelson & Nelson 1097* (UC, WS, PH, US, RM).

2. *Phacelia lenta* Piper. Bull. Tor. Bot. Club. 28:44. 1901.

Glandular perennial; 1-1.5 dm tall; leaves 1.5-6 cm. long, the lower long-petiolate, the upper sub-sessile, blades oblong-elliptic and pinnatifid, the 5-9 divisions cleft into 2-5 lobes; inflorescence 3-7 cm long, with ascending cymes, the flowers with pedicels 1-3 mm long; calyces glandular, linear-lanceolate, 4-6 mm long; corolla persistent, white, 6-8 mm long and cleft 1/3 its length into rounded lobes, inner surface pubescent; stamens 15-20 mm long, with glabrous filaments; style equal to stamens, cleft 1/4 its length; capsule equal to ensheathing corolla; seeds, 15-20, black, ca. 1 mm long.

TYPE: "Bare hills of Columbia River, Washington Territory, May, 1883". *T.S. Brandegee 976* (GH!) Isotypes (CAN! UC!).

This species is known only from the type collection, and may possibly be extinct. The distinctive seeds and colletes (Figs. 2, 3), and restricted distribution indicate that Piper was correct in giving this material specific rank. It is by no means an aberrant form of *P. sericea* as suggested by Brand (1913).

Piper (1906) cites *Brandegee 975* (*Phacelia ramosissima*), from Priest Rapids, on the Columbia; and *Brandegee 978* (*Nama parviflorum*) collected near Wallula, about 75 miles downstream. The type collection of *P. lenta*, therefore, may have been obtained between these points.

3. *Phacelia Lyallii* (A. Gray) Rydberg. Mem. N.Y. Bot. Gard. 1: 325. 1900.

Phacelia sericea (Graham) A. Gray var. *Lyallii* A. Gray. Proc. Am. Acad. 10: 323. 1875.

Phacelia sericea subsp. *Lyallii* (A. Gray) Brand in Engler, Pflanzenreich 4²⁵¹: 107. 1913.

Variously branched, strigose-pubescent perennial; lower branches frequently rhizomatous in talus plants; leaves 2-12 cm long, lamina lanceolate to ovate, coarsely dentate to pinnatifid; lower leaves long-petiolate, upper leaves sessile; leafy inflorescence axis terminating in a single helicoid cyme, or in several near equal branches each bearing

1-2 cymes; calyces linear, 3-8 mm long; corolla deciduous, 5-8 mm long, purple to lavender, rarely white, open-campanulate, cleft about 1/3 its length into rounded lobes, pubescent on inner surface; stamens exerted up to twice the length of corolla, the filaments glabrous; style nearly equal to stamens, cleft 1/4 to 1/3 its length; capsule 5-8 mm long, with acute tip, seeds 12-20, black, ca. 1.5 mm long.

TYPE: "Rocky Mts. Lat 49° N. Alt. 6-7000 ft. above the sea. 1861." *Lyall s.n.* (GH!)

RANGE: Restricted to talus banks and rock crevices on and near summits of the northern Rocky Mountains, 5,000-11,000 feet, southwestern Montana to southern Alberta (Fig. 4).

This species is sympatric with *Phacelia sericea* subsp. *sericea* in Glacier National Park, Montana, where distinctive plants of each occur within a few feet of each other. The two species are similar in leaf shape and in corolla morphology (Fig. 1); but are quite different in seed and embryo features (Fig. 2), as well as in the size of non-glandular hairs.

The crisp, fleshy leaves of plants in the natural habitat (Logan Pass, Montana) are very probably a result of environmental modification, for greenhouse plants of the same race produced pliable, non-fleshy leaves.

ALBERTA: Waterton Lakes National Park: Lower Carthew Lake, *Hitchcock & Martin 18438* (GH, WS, UC). MONTANA: Glacier Co.: Grinnell Lake, *Hitchcock 1988* (NY). Flathead Co.: Gordon Mountain, *Hitchcock 18882* (RM, UC, WS, NY, COLO, ID). Beaverhead Co.: Lake Waukena, *Hitchcock & Muhlick 13060* (GH, RM, UC, WS, NY, CAS, CAN). IDAHO: Lemhi Co.: Bitter Root Range, *Kirtley s.n.* (WS); Mill Creek, Salmon River Mts., *Henderson 3945* (RM).

4. *Phacelia mollis* Macbride. Contr. Gray Herb. 49: 39. 1917.

Velutinous perennial 1-6 dm tall; pubescence of long, spreading, often twisted, non-glandular hairs, and interspersed short glandular hairs; vegetative axis very short, bearing numerous leaves, 1-25 cm long, petiolate; lamina lanceolate, 1-15 cm long, coarsely toothed to lobed to pinnatifid, the divisions entire or with 1-3 shallow clefts; inflorescence virgate, the stout axis with few sessile leaves below; bearing slender, leafless branches up to 15 cm long, each branch giving rise to 1-7 helicoid cymes 1-3 cm long; flowers on slender pedicels 1-5 mm long; calyces linear, 4-8 mm long; corolla deciduous, campanulate, 5-10 mm long, cleft about 1/3 its length into rounded lobes; stamens about twice the length of corolla, inserted slightly above base of tube, the filaments glabrous, bases free of corolla scales; style equal to stamens, cleft from 1/5 to 1/4 its length; capsule 5-10 mm long, the beak acute to acuminate; seeds 20-35, black, ca. 1.5 mm long.

TYPE: Coffee Creek, Yukon Territory *Eastwood 551-a* (US!) Isotype (CAS!)

RANGE: Dawson Range, Alaska and Yukon Territory, with outlying population near Haines, Alaska; sea level to 5500 feet (Fig. 4).

This species occurs on exposed sites, the soil often gravelly, between 60° and 64° north latitude.

Greenhouse plants of *Phacelia mollis* produced vigorous growth only after the use of distilled water and frequent dosages of iron sulfate. These cultural requirements, not necessary for the other species, would suggest that the restricted distribution of *P. mollis* could be due, in part, to specific soil requirements.

ALASKA: Chicken, *Smith 2407* (MSC, UC); Milepost 1260, Alaska Highway, *Williams s.n.* (S); Klukwan, *Anderson 2196* (NY). YUKON: Klotassin, *Cairnes s.n.* (CAN, NY); Dawson Range, *Bostock 10* (CAN); Selwyn River, *Tarleton 145* (US); Ladue Valley, *Eaton s.n.* (US).

5. *Phacelia idahoensis* Henderson. Bull. Torr. Bot. Club. 22:48. 1895.

Phacelia sericea subsp. *idahoensis* (Henderson) Brand in Engler, Pflanzenreich 4²⁵¹: 107. 1913.

Glabrate perennial with pubescence of scattered, appressed hairs, and few interspersed colleters; vegetative axis from 2-5 cm long, often branched; the floriferous meristem arising directly from the leaf rosette and elevated by sub-terminal growth to form a virgate, fistulose inflorescence axis; basal leaves up to 20 cm long, with petioles equal to or shorter than the lamina, the upper leaves progressively shorter-petiolate to sessile-bracteate; lamina lanceolate to ovate, entire to cleft to pinnatifid to lobed, the primary divisions up to 1 cm broad, these entire or cleft into 2-3 lobes; inflorescence axis up to 1.5 m high, leafy below; the terminal floriferous portion up to 4 dm long; the axis giving rise to small branches 5-15 mm long, each bearing a pair of helicoid cymes 5-15 mm long, each with 2-7 flowers on slender pedicels 2-5 mm long; calyces linear, 3-5 mm long; corolla persistent, 4-6 mm long, urceolate, white to light purple, cleft 1/4 to 1/3 its length into rounded lobes, inner surface pubescent between lateral traces of each lobe; the tube strongly dilated between the lateral traces of each lobe to form 5 gibbous nectaries, each nectary covered by a pair of overlapping, parallel corolla scales; stamens with glabrous filaments ca. 1 1/4 length of corolla, the bases free of corolla scales; style included to exerted up to 5 mm above corolla, cleft 1/5 to 1/3 its length; capsule equal to and ensheathed by the marcescent corolla, the beak short-acuminate; seeds 20-30, black, 1-2 mm long.

TYPE: Craig Mts., Nez Perce Co., Idaho. *Henderson 2770* (US). Isotypes (RM! MSC! WS (incl. photo of type)!)

RANGE: Central Idaho, in wet meadows, streambanks, and partially-flooded areas, 2800 to 7000 feet (Fig. 5).

Its unique floral morphology and restriction to wet habitats within a relatively limited geographical area, make

Phacelia idahoensis an easily recognized species. It is relatively uniform throughout its range in contrast to extensive variation found in the closely related *P. sericea*.

IDAHO: Latah Co.: Boville, *Piper 2902* (GH, WS). Shoshone Co.: Cranberry Creek, *Sharsmith 3586* (RM, GH, CAS, UC, WS). Idaho Co.: Orogrande, *Leiberg 1024* (UC, RM, GH, CAS). Valley Co.: Warm Lake, *Hitchcock & Muhlick 14022* (RM, UC, WS, CAS). Custer Co.: Stanley, *Hitchcock 19182* (CAN, WS, UC, RM, COLO, ID). Boise Co.: Beaver Creek, *Hitchcock & Muhlick 9983* (UC, WS).

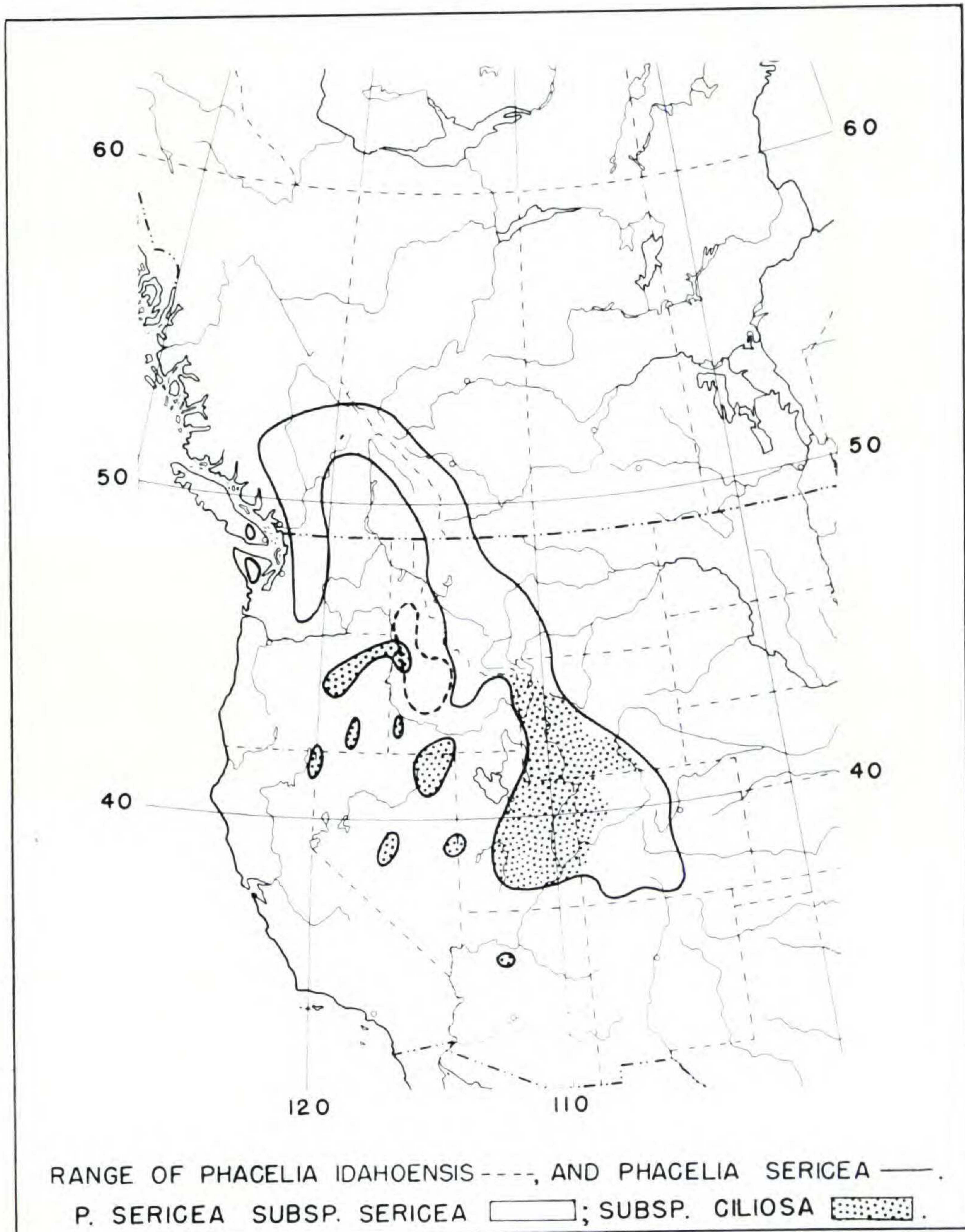


FIG. 5. Geographical distribution of *Phacelia idahoensis* and *P. sericea*.

6. *Phacelia sericea* (Graham) A. Gray. Amer. Journ. Sci. II. 34: 254. 1862.

Eutoca sericea Graham. Edinburgh N. Phil. Journ. 172. 1830. Bot. Mag. 57: pl. 3003. 1830.

Sericeous perennial up to 0.6 m tall with pubescence of numerous fine, appressed hairs and interspersed colleters; vegetative axis from 2-5 cm long, often branched; the floriferous meristem arising directly from the leaf rosette and elevated by sub-terminal growth to form a virgate fistulose inflorescence axis; basal leaves up to 20 cm long, with petioles equal to or shorter than the lamina, the upper leaves progressively shorter-petiolate to sessile-bracteate; lamina lanceolate to ovate, cleft to pinnatifid to lobed, the primary divisions 1-10 mm broad, entire or cleft into 2-5 narrow lobes; inflorescence axis up to 0.6 m high, leafy below; the terminal floriferous portion up to 2.5 dm long; the axis giving rise to small branches 5-15 mm long, each branch bearing one or two helicoid cymes up to 3 cm long, each bearing from 2-7 flowers on slender pedicels 2-5 mm long; calyces linear, 5-7 mm long; corolla persistent, 5-8 mm long, urceolate-campanulate to campanulate, light to dark purple, cleft $1/3$ to $1/2$ its length into rounded lobes, inner surface pubescent between lateral traces of each lobe; the tube dilated to slightly concave between lateral traces of each lobe to form 5 nectaries; each nectary covered by a pair of overlapping, parallel scales; stamens with glabrous filaments ca. $1\frac{1}{4}$ -3 times length of corolla, the bases free of corolla scales; style slightly shorter, equal to, or longer than stamens, cleft $1/5$ to $1/3$ its length; capsule equal to and ensheathed by the marcescent corolla, the beak acuminate; seeds 20-40, black, 1-2 mm long.

6-A. *Phacelia sericea* subsp. *sericea*.

Phacelia sericea (Graham) A. Gray subsp. *eu-sericea* var. *caespitosa* Brand in Pflanzenreich 4²⁵¹: 107. 1913.

Dense to matted-sericeous plants up to 0.5 m tall; basal and upper leaves cleft to pinnatifid to lobed, the divisions 1-5 mm broad; cymes congested on inflorescence axis; corollas campanulate with shallow nectaries, stamens 2-3 times the length of corolla.

TYPE AREA: Canadian Rockies (Drummond, 2nd Franklin Exped.).

RANGE: Rocky Mountains, Cascades, and Olympic Range, 4500 to 13000 feet (Fig. 5).

This subspecies occurs on a wide variety of montane habitats, very frequently above timberline. Populations in the Cascade Mountains, the Olympic Range and the far-northern Rockies are restricted to alpine habitats; and this habitat restriction is correlated with a generally uniform flower shape (campanulate), pubescence (matted-sericeous), and leaf-cutting (narrow lobes). Plants of the northern, central, and southern Rocky Mountains occur on sub-alpine to alpine habitats, and demonstrate much greater variability in these

three features, portraying a gradual intergradation of subsp. *sericea* with subsp. *ciliosa*. In central Wyoming, this intergradation can be seen in plants of the same population.

WASHINGTON: Callam Co.: Obstruction Point Ridge, *Meyer 1234* (UC, COLO, WS, GH). Okanogan Co.: Harts Pass, *Kruckeberg 2678* (RM, WS, CAN, ID, UC, COLO). BRITISH COLUMBIA: Natal, *Weber 2286* (COLO, UC, WS, RM, GH). ALBERTA: Pincher Creek, *Moss 805* (GH, UC). MONTANA: Lake Co.: McDonald Lake, *Hitchcock 18215* (CAS, WS, RM, UC, ID, COLO). Park Co.: Silver Pass, *Hitchcock 16415* (COLO, RM, GH, UC, WS). IDAHO: Blaine Co.: Norton Peak, *Hitchcock & Muhlick 10683* (CAN, RM, UC, WS, GH, CAS). WYOMING: Park Co.: Sylvan Pass, *Gillett 1149* (MSC, UC). Albany Co.: Woods Creek, *Goodding 1434* (UC, COLO, RM, GH). COLORADO: Clear Creek Co. Loveland Pass, *Robbins 738* (COLO, UC, GH). Hinsdale Co.: Carson, *Baker 304* (GH, CAS, UC, WS, RM). La Plata Co.: La Plata, *Baker 520* (GH, CAS, UC, RM). Mineral Co.: Wolf Creek Pass, *Beaman 1128* (MSC).

6-B. *Phacelia sericea* subsp. *ciliosa* (Rydb.) stat. nov.

Phacelia sericea var. *ciliosa* Rydberg. Bull. Tor. Bot. Club 31: 636. 1904.

Phacelia sericea (Graham) A. Gray subsp. *eu-sericea* var. *biennis* (A. Nelson) Brand in Engler, Pflanzenreich 4²⁵¹: 107. 1913. (As to name only).

Phacelia sericea (Graham) A. Gray subsp. *eu-sericea* var. *Nelsoni* Brand. op. cit. 107. 1913.

Glabrate to sericeous plants up to 0.6 m tall; basal and upper leaves cleft to pinnatifid to lobed, the divisions 3-10 mm broad; cymes congested to sparsely distributed on inflorescence axis; corollas urceolate-campanulate, with slightly gibbous nectaries; stamens 1 1/4-2 times length of corolla.

TYPE: North of Meeker, Rio Blanco Co., Colorado. *Osterhout 2619* (NY!). Isotype (RM!).

RANGE: Isolated mountain ranges, Wallowa Mts., Oregon to San Francisco Peaks, Arizona; and Warner Mts., California to Laramie Mts., Wyoming; 6,000 to 11,500 feet (Fig. 5).

This subspecies includes material that portrays a very broad spectrum of variation. This variation is quantitative, and is conspicuously expressed by the amount of pubescence, the width of leaf lobes, and the shape of the corolla (cf. Gillett, In Press). One extreme of this variation is portrayed by specimens that show a resemblance to *Phacelia idahoensis*. At the other extreme, specimens bear a very marked resemblance to *P. sericea* subsp. *sericea*. Because of the gradual intergradation between this material and the sympatric *P. sericea* subsp. *sericea*, this assemblage of intermediate forms is considered best aligned with *P. sericea*

rather than *P. idahoensis*.

OREGON: Baker Co.: Anthony Lakes, *Hitchcock 19702* (MONTU, UC, RM, ID, WS, CAS). Wallowa Co.: Aneroid Lake, *Kruckeberg 3141* (WS, ID, UC, RM, CAS, MONTU). Harney Co.: Steens Mts., *Thompson 12134* (UC, CAS, GH). IDAHO: Idaho Co.: Heavens Gate, *Jones 193* (ID, WS, GH). OWYHEE CO.: Silver City, *Macbride 901* (CAN, GH, ID, WS, RM, UC). CALIFORNIA: Modoc Co.: Head of Eagle Creek, *Alexander & Kellogg 5090* (UC, GH). NEVADA: Elko Co.: Jarbidge, *Nelson & Macbride 1929* (RM, MONTU, ID, UC, GH). Nye Co.: Mohawk R. S., *Linsdale 217* (CAS). White Pine Co.: Lehman Basin, *Maguire 21130* (UC, CAS). UTAH: Uintah Co.: Vernal, *Porter & Rollins 5631* (GH, RM, UC). San Juan Co.: Abajo Mts., *Goodman & Hitchcock 1380* (RM, MONTU, CAS, GH, UC). WYOMING: Uinta Co.: Evanston, *Rollins 2346* (GH, UC). Sublette Co.: Green River Lakes, *Porter 5508* (GH, CAS, RM). Albany Co.: Woods Creek, *Goodding 1434* (GH, UC). COLORADO: Moffatt Co.: Cold Spring Mt., *Porter 3928* (RM, GH). ARIZONA: Coconino Co.: Near Flagstaff, *Purpus s.n.* (UC). — DEPARTMENT OF BOTANY AND PLANT PATHOLOGY, MICHIGAN STATE UNIVERSITY.

LITERATURE CITED

- BRAND, A. 1913. Hydrophyllaceae. *In* A. Engler, *Pflanzenreich* 4²⁵¹: 1-210.
- CAVE, M. S. AND L. CONSTANCE. 1942, 1944, 1947, 1950, and 1959. Chromosome numbers in the Hydrophyllaceae. *Univ. Calif. Publ. Bot.* 18: 205-216; 293-298; and 449-465. 23: 363-382. 30: 233-258.
- CONSTANCE, L. 1949. A revision of *Phacelia* subgenus *Cosmanthus* (Hydrophyllaceae). *Contr. Gray Herb.* 168: 1-48.
- . 1951. Hydrophyllaceae. *In* L. R. Abrams. *Illustrated Flora of the Pacific States.* 3: 476-532. Stanford University Press.
- GILLETT, G. W. 1955. Variation and genetic relationships in the *Whitlavia* and *Gymnobythus phacelias*. *Univ. Calif. Publ. Bot.* 28: 19-78.
- . *In Press.* An experimental study of variation in the *Phacelia sericea* complex. *Amer. Journ. Bot.*
- GRAY, A. 1875. A conspectus of the North American Hydrophyllaceae. *Proc. Amer. Acad.*, 10: 312-332.
- HECKARD, L. R. 1960. Taxonomic studies in the *Phacelia magellanica* polyploid complex. *Univ. Calif. Publ. Bot.* 32: 1-126.
- HOWELL, J. T. 1945. Studies in *Phacelia* — revision of species related to *P. Douglasii*, *P. linearis*, and *P. Pringlei*. *Amer. Midl. Nat.* 33: 460-494.
- LANJOUW, J. AND F. A. STAFLEU. 1959. *Index Herbariorum.* 4th ed. Pt. 1 The Herbaria of the World. 1-249.
- MARTIN, A. C. 1946. The comparative internal morphology of seeds. *Amer. Midl. Nat.* 36: 513-660.
- PIPER, C. V. 1906. *Flora of the State of Washington.* *Contr. U. S. Nat. Herb.* 9: 5-637.

HEPATICA IN NORTH AMERICA

JULIAN A. STEYERMARK AND CORA S. STEYERMARK

For many years North American botanists have accepted the maintenance of two species of *Hepatica* in the United States and Canada, *H. acutiloba* DC. and *H. americana* (DC.) Ker. This division into distinct specific taxa has been continued in the current eighth edition of Gray's Manual. However, Gleason, in the New Illustrated Flora (vol. 2: 183. 1952) has questioned the soundness of the recognition of *H. americana* as a species distinct from *H. nobilis* Schreb. of Europe, noting that "The difference between our plant and the European *H. nobilis* Schreb. is slight and scarcely warrants specific segregation." It is the purpose of the present paper to provide further support of Gleason's suggestion, and to bring evidence to indicate that the American taxa of *Hepatica* are better considered as varieties of the European *H. nobilis*.

PRELIMINARY OBSERVATIONS

North American *Hepaticas* fall naturally into two taxa, 1) those with rounded lobes of the leaf-blades, and 2) those with acute or acutish lobes. These obvious differences have been the chief criteria used to distinguish the taxa specifically. Over most of the North American range of the genus, the two taxa occupy usually separate and distinct habitats, the populations of the two taxa maintaining themselves rather uniformly, not only ecologically but also geographically. In Missouri, for example, *H. acutiloba* DC. occupies the more neutral to calcareous soils, *H. americana* the more acid soils, and *H. acutiloba* occupies glaciated northern Missouri extending west in that sector to Mercer and Sullivan counties, whereas *H. americana* is restricted to unglaciated Ozarkian southern Missouri. The ranges of the two taxa in Missouri are fairly sharp, but at their zones of overlap geographically and ecologically intergrading specimens of hybrid origin are encountered (Fig. 1). In northern Illinois, where the margins of the ranges also overlap, intermediate types are found which are impossible to assign to one or the other of the two taxa.

The problem of the recognition of the two taxa as distinct

species presented itself to the present authors in 1943. Both "species" occurred by the thousands on the forested morainal slopes and crests of the ravines of the Valparaiso Moraine in the area where the authors lived in the Biltmore subdivision of Barrington, Lake County, northern Illinois. The opportunity of intensive study of this problem was offered the junior author, who intensively surveyed the living flowering plants throughout a three-mile length of the stream

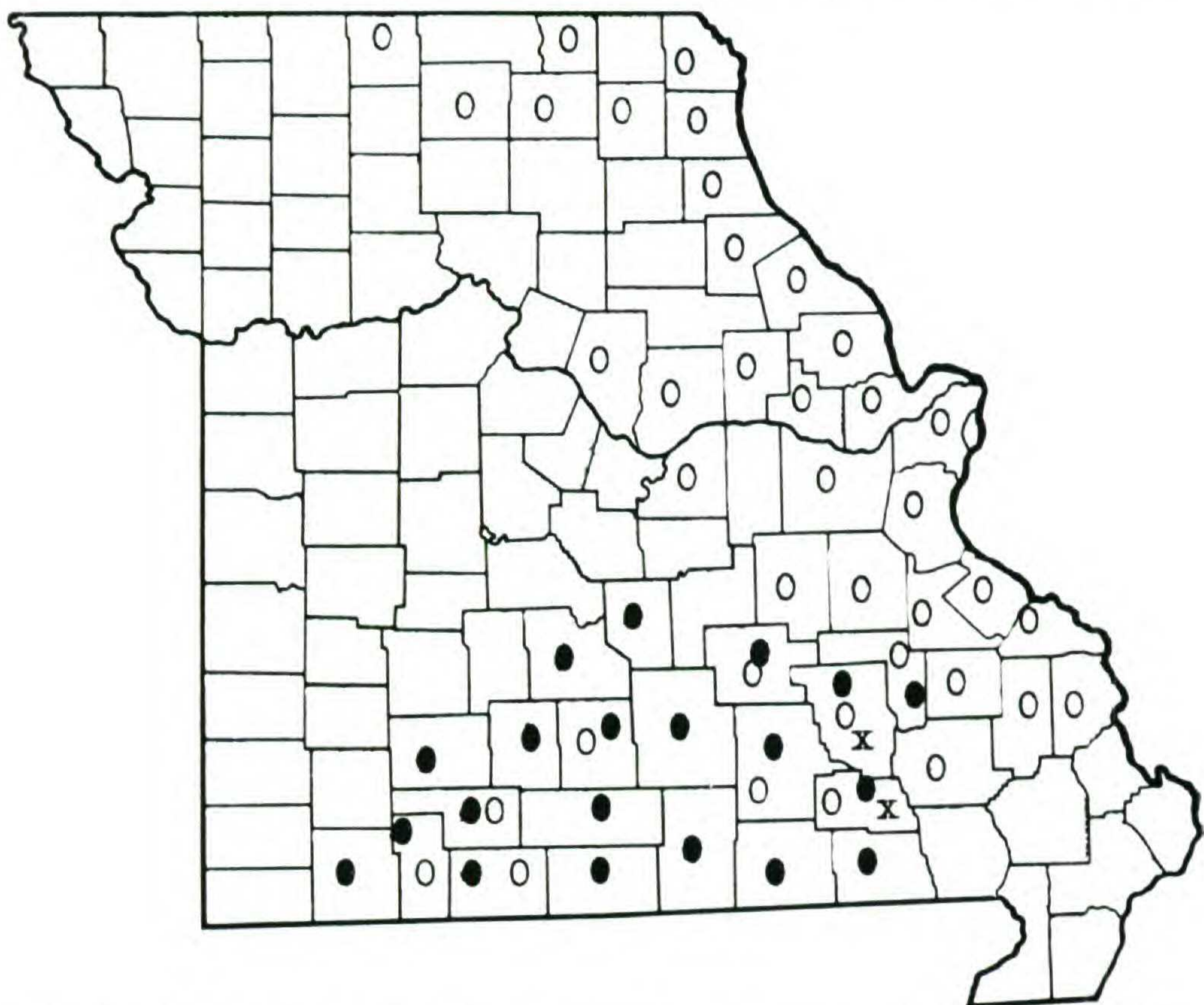


FIG. 1. Distribution of *Hepatica* in Missouri. Solid oval — *H. nobilis* var. *obtusa*. Open oval — *H. nobilis* var. *acuta*. X — putative hybrid populations.

following Eton Drive in the wooded section of Biltmore subdivision. In this area *H. americana* occurred on the more acid, leached soils on top of the ravines and slopes, whereas *H. acutiloba* was encountered most frequently in the richer and more neutral soil of the creek bottom and ascended to nearly three-fourths the distance up the slope. A zone of overlap existed in the upper portion of the slope where the two types met. Study of all the plants in this extensive area, based upon apex of leaf-blades and involucre, revealed an intergradation of the two taxa, showing the following results: 35% pure *H. americana*, 15% pure *H. acutiloba*, with

the remaining 50% somewhere between the two and often too puzzling to determine as one or the other "species." No additional facts could be obtained from study of the color, number, length, or width of the sepals. Their color varied from pale lavender to deep purple in 90% of the plants examined, pale pink to deep rose in about 5% of the cases, and white in another 5%. Both taxa exhibited approximately the same percentage differences. Moreover, no distinction could be found among either *H. acutiloba* or *H. americana* in color variation nor in their occurrence on any particular exposure of slope.

Measurements of involucre and sepals of living plants from the above area revealed the following: *Sepal length*: 9-13 mm. long in *H. americana*, averaging 11.6 mm.; 10-15 mm. long in *H. acutiloba*, averaging 11.75 mm.; 11-14 mm. long in the intermediate types, averaging 12.05 mm. *Sepal width*: 5.5-8 mm. wide in *H. americana*, averaging 6.5 mm.; 4-8 mm. wide in *H. acutiloba*, averaging 6.75 mm.; 5.5-10 mm. wide in the intermediate types, averaging 7.15 mm. *Involucre length*: 9-17 mm. long in *H. americana*, averaging 12.3 mm.; 7-18 mm. long in *H. acutiloba*, averaging 11.4 mm.; 9-14 mm. long in the intermediate types, averaging 11.4 mm. *Involucre width*: 7.5-9 mm. wide in *H. americana*, averaging 7.25 mm.; 4-9 mm. wide in *H. acutiloba*, averaging 5.95 mm.; 4.5-9 mm. wide in the intermediate types, averaging 6.65 mm. The averages of these measurements are summarized as follows:

	<i>H. americana</i>	<i>H. acutiloba</i>	<i>Intermediate</i>
Sepal length	11.6	11.75	12.05
Sepal width	6.5	6.75	7.15
Involucre length	12.3	11.4	11.4
Involucre width	7.25	5.95	6.65

Preliminary cytological studies conducted by Dr. O. J. Eigsti and Dr. Albert S. Rouffa revealed no conclusive differences between the two taxa.

STUDY OF HERBARIUM MATERIAL

In order to determine the relationship of North American *Hepatica* to other taxa of the genus, especially those involving the closely related *Hepatica nobilis*, specimens were studied by the senior author from the following herbaria: Chicago Natural History Museum, Gray Herbarium of Har-

vard University, Missouri Botanical Garden, and United States National Herbarium. To the curators of these institutions the senior author is deeply grateful for the privilege of studying this material. Criteria used for study involved length and pubescence of petioles, length and width of involucre and sepals, relative pubescence of leaf-blades and involucre, and shape and pubescence of achenes. Specimens of *Hepatica* from North America were compared with those from Europe and eastern Asia.

In Europe *Hepatica nobilis* consists of two main variations, (1) the more common type, with the lobes of the leaf-blades usually acute or short-pointed or acutish, and (2) a less frequent type, with the lobes of the leaf-blades usually rounded. The historical type is based upon the variation with acutish lobes and is the same as *Anemone Hepatica* L. var. *typica* (Beck) Gürke, *A. Hepatica* var. *acutiuscula* Pritzel, and *H. nobilis* var. *typica* Beck; the round-lobed variation is synonymous with *Anemone Hepatica* var. *rotundata* (Schur.) Gürke and *H. nobilis* var. *rotundata* (Schur.) Domin & Krajina. Since European authors are not in complete agreement as to whether such variations are forms or varieties of *Hepatica nobilis*, references to the European variations are indicated in the discussion below as round-lobed European *H. nobilis* and acute-lobed European *H. nobilis*.

Leaf-blade. Among the European collections of *H. nobilis* examined, about an equal number were either round-lobed or acute-lobed. Among the latter, a number of specimens are on the border line and have an appearance intermediate in aspect between *H. acutiloba* and *H. americana*. Among the round-lobed leaf-blades of the European *H. nobilis* are also a number of border line cases which exhibit a slight acuteness of the lobes. In some specimens, both types of leaf-lobes appeared on the same sheet (herb. *J. S. Mill*, May, 1839, Austria, in Gray Herbarium).

In general, the lobes of the leaf-blades of the American plants of *Hepatica* are sufficiently well-differentiated to enable one to distinguish two types (1) those with the lobes rounded at the summit and usually broader than long, the length of the leaf-blade being about two times the distance

from the base of the sinuses to the summit of the petiole, the usually accepted characteristics of *H. americana*, and (2) those with the lobes acute or acutish at the summit and usually longer than broad, the length of the leaf-blade being about three times the distance from the base of the sinuses to the summit of the petiole, the usually accepted characteristics of *H. acutiloba*. In various parts of the range where the two taxa meet, putative hybrids are encountered which cannot be placed in either *H. acutiloba* or *H. americana*. An example of this is represented by the collection of *Steyermark* 73114 from Reynolds County, Missouri (steep, north-facing wooded slopes along West Fork of Black River, T 32 N, R 2 W, sec. 1, southeast of West Fork P. O., 7½ mi. northeast of Bunker, April 26, 1952, in herb. Chi. Nat. Hist. Mus.). At this locality the uppermost acid chert slopes are occupied by *H. americana*, while the lower and middle limestone slopes are inhabited by *H. acutiloba*. Similar intermediate hybrid specimens were found in Carter County, Missouri, where both taxa are present, and in Lake County, northern Illinois, where the problem of intermediate plants presented itself to the authors at the outset of this study.

Forms of acute-lobed *H. nobilis* of Europe often resemble specimens of *H. acutiloba*, and, similarly, forms of round-lobed *H. nobilis* of Europe often markedly resemble plants of *H. americana*. It is, therefore, a matter of difficulty to distinguish some of the European forms of *H. nobilis* from one or the other of the two American taxa.

Petioles and scapes. Length of the petioles in *H. americana* varies from 4-15 cm. long in flowering specimens. In both the round-lobed and acute-lobed forms of *H. nobilis* of Europe, the petioles vary from 3-17 cm. long in flowering material. In *H. acutiloba* the petioles are slightly longer, varying from 6-20 cm. long.

The scapes of European *H. nobilis* in flowering specimens average somewhat longer than those of the American plants, equaling or surpassing the length of the petioles. The petioles and scapes of the European *H. nobilis* are usually less pubescent than those of the American plants, and especially of *H. americana*.

Sepal length. With respect to the length of the sepals, the